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THE UNIVERSITY OF ALBERTA

COMPARATIVE CRANIAL OSTEOLOGY OF THE STICKLEBACKS,
Culaea inconstans (Kirtland), *Pungitius pungitius*
(Linnaeus), and *Apeltes quadracus* (Mitchill)
(family Gasterosteidae)

by



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The undersigned certify that they have read,
and recommend to the Faculty of Graduate Studies and
Research for acceptance, a thesis entitled "Comparative
cranial osteology of the sticklebacks, *Culaea inconstans*
(Kirtland), *Pungitius pungitius* (Linnaeus), and *Apeltes*
quadracus (Mitchill) (family Gasterosteidae)" submitted
by Rassmee Sroivattana in partial fulfilment of the
requirements for the degree of Master of Science.

ABSTRACT

The comparative cranial osteology of three species of sticklebacks, *Culaea inconstans*, *Pungitius pungitius*, and *Apeltes quadracus* was studied in detail. The material was stained and cleared with an enzyme technique. Details of the comparative morphology of the cranial osteology were carefully studied by dissecting the specimens under a dissecting microscope. Drawings were made with the aid of a camera lucida on a Wild M-5 microscope. Standard length of the specimens was measured in mm. with dial calipers.

No cranial bone is unique to any of the three species. The only differences in bones are morphological differences and differences in number.

The distinctive morphological features of each species are characterized by the following: *Culaea*, the single-ethmoid bone is small with a lateral wing-like process; the lachrymal bears a deep indentation on the antero-dorsal surface; the last suborbital possesses several shallow lobes along the posterior margin; the entopterygoid does not reach the symplectic floor. *Pungitius*, the single ethmoid is oval-shaped; the last suborbital is dichotomously branched on the posterior margin; gill rakers are conspicuously long. *Apeltes*, the ethmoid is short; the vomer head is long and rectangular; the last suborbital has a pointed end; the angular possesses a blunt postero-dorsal process and the process of dentary is overlapped by the angular process.

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INTRODUCTION

Many detailed osteological studies have been made on fish (e.g., Gosline, 1951, 1961; Grégory, 1933; Harrington, 1955; Liem, 1963; Marathe, 1959; Norden, 1961; Regan, 1913; Srinivasachar, 1955; Vladykov, 1962; Weitzman, 1962). Amongst the members of the family Gasterosteidae (sticklebacks), only the osteology of the threespine stickleback *Gasterosteus aculeatus* (Linnaeus) has been studied in much detail (e.g., Kampf, 1961; Swinnerton, 1902). Nelson (1971) made a detailed comparison of the pectoral and pelvic skeletons and of some other bones (including several in the head) in all gasterosteid species but few or no detailed studies have been made on the cranial osteology of the brook stickleback (*Culaea inconstans* (Kirtland)), the ninespine stickleback (*Pungitius pungitius* (Linnaeus)), and the four-spine stickleback (*Apeltes quadracus* (Mitchill)).

Studies on cranial osteology are important because they may provide a basis for constructing a sound phylogeny of a group. Phylogenetic conclusions, however, are not attempted here because a comparative study of the entire family was not attempted.

The phylogenetic placement of sticklebacks is much disputed (perhaps because of a lack of detailed comparative studies). Greenwood *et al.* (1966) classifies them as follows: Division III, Superorder Acanthopterygii, Order Gasterosteiformes, and Suborder Gasterosteoides (with three

families - however, Banister, 1970, has shown that the Indostomids do not belong here).

The objectives of this study are as follows:

1. To present a check-list of the bones in gasterosteids.
2. To present an illustrated description of the osteology of the head of *Culaea inconstans*, *Pungitius pungitius*, and *Apeltes quadracus*.
3. To compare some of the head bones of these three species, *Culaea inconstans*, *Pungitius pungitius*, and *Apeltes quadracus*.

MATERIALS AND METHODS

Source of Material

Brook sticklebacks were collected from Residence Point, Astotin Lake (Fig. 1, 2). A small-mesh seine net was used to collect the specimens. The fish were fixed immediately in 10% formalin, then later transferred to 40% isopropyl alcohol. Residence Point is a shallow bay with soft mud and organic debris on the bottom with a few scattered areas of sand. A beaver lodge is located near the collection site. Trees occur around the shoreline.

Astotin Lake is located at the north end of Elk Island National Park, which is situated in the Beaver Hills of central Alberta. It is the largest lake in Elk Island National Park and has a maximum depth of 23 feet (7 m.). The lake centre lies at longitude $112^{\circ} 51'$ West and latitude $53^{\circ} 41'$ North. The city of Edmonton is twenty-five miles (40 km.) west of the lake.

Ninespine sticklebacks were obtained from the Museum of Zoology, The University of Alberta. All were collected in North America (primarily Indiana and Alberta).

Fourspine sticklebacks were also from collections housed in the University of Alberta, Museum of Zoology. They were collected from Pennsylvania in the Big Spring Run stream in 1967 by Dr. J. S. Nelson. The population is an introduced one from the Atlantic coast of North America but

is now confined to freshwater.

Method of Staining and Clearing

A sample of specimens was stained with alizarin red-S and cleared according to the trypsin enzyme digestion technique described by Taylor (1967). They were then placed in glycerine (to which some thymol was added).

Method of Study

Details of the comparative morphology of the cranial osteology were carefully studied by dissecting the specimens under a dissecting microscope. Drawings were made with the aid of a camera lucida on a Wild M-5 microscope. Standard length of the study specimens was measured in mm. with dial calipers (the standard length of the study specimens ranged from 33 mm. to 52 mm.).

The descriptive osteology has been detailed on the following different cranial skeleton regions:

- I. Nasal region
- II. Orbital region
- III. Otic region
- IV. Basicranial region
- V. Branchiocranium
 - A. Hyobranchial region
 - B. Opercular series
- VI. Oromandibular region

RESULTS

Check List

The following is a check list of the cranial skeleton in gasterosteids. The names marked with an asterisk are single (unpaired) bones.

I. Nasal region

1. nasal
2. mes-ethmoid
3. lateral ethmoid
4. single ethmoid*
5. vomer head*

II. Orbital region

6. frontals
7. lachrymal
8. suborbitals

III. Otic region

9. sphenotic
10. pterotic (supratemporal
11. parietal
12. prootic
13. epiotic
14. posttemporal
15. supracleithrum
16. intercalary

17. supraoccipital*

18. exoccipital

IV. Basicranial region

19. basioccipital*

20. para-sphenoid*

(20)a. lateral process of parasphenoid

(20)b. pharyngeal process of parasphenoid

V. Branchiocranium

A. Hyabranhial region

21. interhyal

22. epi-hyal

23. ceratohyal

24. hypohyal

(24)a. dorsal hypohyal

(24)b. ventral hypohyal

25. basihyal (glossohyal)*

26. posterior basihyal*

27. urohyal

28. brancheostegal rays

29. basibranchials

30. hypobranchials

31. ceratobranchials

(31)a. gill rakers

32. epibranchials

33. pharyngo branchials

B. Opercular series

- 34. opercular
- 35. subopercular
- 36. interopercular
- 37. preopercular

VI. Oromandibular region

The oromandibular bones are movably suspended from the neurocranium by the palatines anteriorly and by the hyomandibulars posteriorly.

- 38. palatines
- 39. entopterygoid
- 40. metapterygoid
- 41. symplectic
- 42. quadrate
- 43. hyomandibular
- 44. premaxillary
- 45. maxillary
- 46. angular
- 47. dentary
- 48. retroarticular

Descriptive Osteology

I. Nasal region (Fig. 3, A,B,C; Fig. 5, A,B,C)

Nasal

Culaea inconstans

The nasals are narrow and elongate; there is a slender process curved downwards from the anterior nasal, projecting posteriorly, and lying over the mes-ethmoid (Fig. 3A).

Pungitius pungitius

The nasals are similar to the ones in *Culaea* but the bones are much longer and the ventral processes are larger (Fig. 3B).

Apeltes quadracus

The nasals are identical to the ones found in *Culaea*.

Mes-ethmoid

Culaea inconstans

The mes-ethmoid is an elongate, hook-like bone. The body of the bone is slender. The posterior tip of the bone is joined to the palatine. The anterior mes-ethmoid is curved laterally to form a hook. It is a free floating bone, not sutured to any other bone, but it does touch the antero-dorsal lachrymal. The mes-ethmoid articulates antero-medially with the lateral border of vomer head (Fig. 12A).

Pungitius pungitius

The shape of the mes-ethmoid is similar to *Culaea*; however, the body of the bone is relatively long and slender (Fig. 12B).

Apeltes quadracus

The mes-ethmoid is considerably shorter than in the two previous species (Fig. 12C).

Lateral ethmoid

Culaea inconstans

The lateral ethmoid is a complex bone and fairly well developed. It touches the posterior nasal and anterior frontal where they join. It is seen as one single piece from the lateral aspect (Fig. 5A), but the median view shows an internal projection of this bone which is funnel-shaped. The bone consists of two distinctive parts, the dorsal process touching the antero-ventral frontal, and the ventro medial tip of the funnel which is connected dorsally with the palatine. The lateral ethmoid forms part of the anterior border of the orbit. There are no articular facets. The posterior nasal process lies anterior to the lateral ethmoid and projects slightly below its ventral surface. The posterior nasal and anterior frontal meet above the dorsal aspect of the lateral ethmoid and articulate with it. Ventrally it connects with the palatine. The vomer process and parasphenoid are situated between the ventral margins of the funnels of the two lateral ethmoids; the contact is loose and does not form a joint.

Pungitius pungitius

The lateral ethmoid is more or less similar to that in *Culaea* (Fig. 12B).

Apeltes quadracus

The lateral ethmoid is remarkably well-developed compared with the two species mentioned above. It has two distinctive parts, a large dorsal flap-like part, and a fairly broad part of the ventro-medial lip of the funnel (Fig. 12C).

Ethmoid

Culaea inconstans

The single ethmoid has a nearly vertical body and is somewhat of a circular shaped bone with a lateral wing-like process (Fig. 12A). The wing-like process of the bone touches ventro-laterally the posterior process of the nasals, and is situated between the lateral ethmoids. The single ethmoid is located medially of the vomer process.

Pungitius pungitius

The oval-shaped single ethmoid has a relatively broad part on the dorsal side. The bone does not possess the lateral wing-like process. The single ethmoid is larger than in *Culaea* (Fig. 12B).

Apeltes quadracus

The single ethmoid is a relatively large bone with an oval shape. The bone sits antero-ventrally on the vomer head and laterally articulates with the lateral ethmoids (Fig. 12C).

Vomer

Culaea inconstans

The vomer head is toothless with two prominent dorso-lateral wing-like processes loosely touching the mes-ethmoid and slightly connecting with the antero-ventral surface of the nasal process. Posteriorly, the vomer tapers off into a point which enters a channel at the anterior end of the parasphenoid (Fig. 7A).

Pungitius pungitius

The lateral wing-like process of the vomer is identical to *Culaea* (Fig. 7B).

Apeltes quadracus

The vomer is a somewhat rectangular bone. It appears to be almost twice as long as the vomer in *Culaea* and *Pungitius* (Fig. 7C, Fig. 12C).

II. Orbital region (Fig. 3, A,B,C; Fig. 5 A,B,C; Figs. 8, 9, 10).

Frontal

Culaea inconstans

The frontals form a large portion of the roof of the cranial cavity and the central roof of the margin of the orbital chamber. The bones articulate anteriorly with the posterior nasal and are bounded laterally by the sphenotic, postero-laterally by the parietal, and postero-medially by the supraoccipital. The frontals form one-half of the roof

of the skull (defined here as the distance from anterior end of nasal to posterior end of supra occipital). The anterior end of the frontal is basically narrower than the posterior part which gradually expands posteriorly (it is about three and one-half times wider than the anterior end). A distinct spine appears along the postero-lateral corner. Ventrally, a conspicuous process of the bone can be seen, running in an antero-ventral to postero-lateral direction, which is articulated with the anterior sphenotic (Fig. 3A, Fig. 5A, Fig. 8).

Pungitius pungitius

The frontals form a larger porportion of the cranial roof than in *Culaea*. The prominent spine is on the postero-lateral corner (Fig. 3B, Fig. 5B).

Apeltes quadracus

The frontals are similar to *Culaea* in general appearance. There is no spine-like process on the postero-lateral corner (Fig. 3C, Fig. 5C, Fig. 10).

Lachrymal

Culaea inconstans

The elongated lachrymal is the first orbital bone. It borders the antero-ventral portion of the orbit. The anterior portion of the bone is relatively slender and connects antero-dorsally with the long thin projection of the lateral process of mes-ethmoid. A long, strong prominent dorso-medial process of the lachrymal is

articulated dorsally to the ventral surface of the lateral ethmoid. A deep indentation is readily seen on the antero-dorsal surface (Fig. 8, Fig. 11A).

Pungitius pungitius

The lachrymal is similar to *Culaea* except that the deep indentation on the antero-dorsal surface is absent (Fig. 9, Fig. 11B).

Apeltes quadracus

The lachrymal is identical to the two species above except that the bone is relatively larger and without any deep indentation (Fig. 10, Fig. 11C).

Suborbital

Culaea inconstans

The suborbitals are usually three in number (including the lachrymal). The second suborbital is short and slender. It connects with the last suborbital. The last or third suborbital is relatively broad with several lobes along the ventral margin of the bone (Fig. 11A).

Pungitius pungitius

There are three suborbital (including the lachrymal). The second suborbital is similar in size and appearance to *Culaea*. The last suborbital is dichotomously branched posteriorly (Fig. 11B).

Apeltes quadracus

In most specimens of *Apeltes* there are two suborbitals (including the lachrymal). The last or second suborbital is about the same size as the third suborbital of *Culaea* or

Pungitius. The anterior portion of the bone is broad while the posterior portion is narrow (Fig. 11C).

III. Otic region (Fig. 3 A,B,C; Fig. 4 A,B,C; Fig. 5 A,B,C; Figs 8, 9, 10).

Sphenotic

Culaea inconstans

The sphenotic is a relatively large bone. It forms part of the posterior border of the orbit. The bone is articulated anteriorly with the frontal. A prominent process of the sphenotic projects anteriorly into the orbit region. At its antero-ventral surface there is a shallow depression for an articulation with the anterior head of the hyomandibular. Anteriorly, the bone is articulated with the lateral process of the parasphenoid. The sphenotic is bordered ventrally by the prootic and posteriorly by the pterotic (Fig. 3A, Fig. 5A, Fig. 8).

Pungitius pungitius

The sphenotic is similar to the above species (Fig. 5B, Fig. 9).

Apeltes quadracus

The sphenotic is identical to the two species mentioned above except that the anterior process of the bone is relatively blunt (Fig. 5C, Fig. 10).

Pterotic

Culaea inconstans

The pterotic, referred to as the supra-temporal by Liem (1963), is a large bone with the small anterior projection lying over the posterior end of the sphenotic. The bone possesses a prominent posterior process which extends posteriorly. The antero-ventral surface of the bone possesses a conspicuous shallow depression for articulation with the dorsal head of the hyomandibular. The pterotic is bounded anteriorly by the sphenotic, antero-dorsally by the parietal, postero-dorsally by the epiotic, postero-ventrally by the exoccipital, and antero-ventrally by the prootic (Fig. 3A, Fig. 4A, Fig. 5A, Fig. 8).

Pungitius pungitius

The pterotics (supratemporal) are identical to the previous species (Fig. 3B, Fig. 4B, Fig. 5B, Fig. 9).

Apeltes quadracus

The pterotics are similar to the two species mentioned above (Fig. 3C, Fig. 4C, Fig. 5C, Fig. 10).

Parietal

Culaea inconstans

The parietal appears in dorsal view as a somewhat rectangular and relatively elongate bone. The bone is bounded anteriorly by the frontal, antero-laterally by the sphenotic, ventrally by the pterotic, and posteriorly by the epiotic (Fig. 3A, Fig. 4A, Fig. 5A, Fig. 8).

Pungitius pungitius

The parietal seems to be similar to that of *Culaea* in general appearance (Fig. 3B, Fig. 4B, Fig. 5B, Fig. 9).

Apeltes quadracus

No differences were found between *Apeltes* and the two species mentioned above (Fig. 3C, Fig. 4C, Fig. 5C, Fig. 10).

Prootic

Culaea inconstans

The prootics are very large bones, somewhat pentagonal in shape, and articulating ventro-medially with the pharyngeal process of the parasphenoid. The bone is bounded anteriorly by the lateral process of the parasphenoid, antero-laterally by the sphenotic, postero-laterally by the pterotic, and posteriorly by the exoccipital and basioccipital. The prootic possesses a large foramen antero-ventrally (Fig. 6A).

Pungitius pungitius

The prootic is identical to the same bone in *Culaea*. (Fig. 6B).

Apeltes quadracus

The prootic is similar to the two species mentioned above (Fig. 6C).

Epiotic

Culaea inconstans

The epiotic is a somewhat conical bone, forming the

postero-dorsal corner of the cranium. The bone is bounded anteriorly by the posterior parietal, medially by the lateral borders of supra occipital, laterally by the pterotic, and posteriorly by exoccipital. The epiotic does not reach the foramen magnum (Fig. 3A, Fig. 4A).

Pungitius pungitius

The epiotic is identical to *Culaea* (Fig. 3B, Fig. 4B).

Apeltes quadracus

The epiotic is similar to the two species mentioned above (Fig. 3C, Fig. 4C).

Intercalary

Culaea inconstans

The intercalary is a relatively small bone. It is a somewhat square shaped bone, lying beneath the suture between the pterotic and exoccipital (Fig. 6A).

Pungitius pungitius

The intercalary appears to be similar to the previous species (Fig. 6B).

Apeltes quadracus

The intercalary is similar to the two species mentioned above (Fig. 6C)

Posttemporal and Supracleithrum

The posttemporal and the supracleithrum of the three species have been described in detail by Nelson (1971) and so they are omitted here.

Supra occipital

Culaea inconstans

The supra occipital is maple-leaf-like to hexagonal in general appearance. There is a conspicuous median keel extending postero-dorsally. The supra occipital does not reach the foramen magnum. The bone is bordered anteriorly by the posterior margin of frontals, laterally by parietals and epiotics, and posteriorly by exoccipital (Fig. 3A, Fig. 4A).

Pungitius pungitius

The supra occipital is similar to the *Culaea* except that the process is longer (Fig. 3B).

Apeltes quadracus

The supra occipital is similar to the two species mentioned above. The most noticeable difference is that the dorsal process is a very strong bone, forming a strong spine (Fig. 10).

Exoccipital

Culaea inconstans

The exoccipital is a fairly large curved bone, extending dorso-ventrally. Two foramina can be seen ventrally on each exoccipital (seen in Fig. 6, but not labelled). The left and right postero-dorsal rings of the exoccipital form the large opening of the foramen magnum, located at the posterior end of the cranium. The exoccipital is bounded anteriorly by the epiotic, laterally by the pterotic,

antero-ventrally by the prootic, ventro-medially by the basioccipital, and antero-medially by the supra occipital (Fig. 3A, Fig. 4A).

Pungitius pungitius

The exoccipitals are identical in appearance to *Culaea*, except that the postero-dorsal wings are longer (Fig. 3B).

Apeltes quadracus

The exoccipital is similar to the two species mentioned above. The postero-dorsal wings are relatively short (Fig. 3C).

IV. Basicranial region (Fig. 6, A,B,C)

Basioccipital

Culaea inconstans

The basioccipital is more or less fan-shaped. The posterior end is modified to form a vertebra-like condyle for articulation with the first vertebra. Ventrally, the basioccipital possesses a very long prominent pharyngeal process projecting anteriorly from the posterior end of the bone. Nearly half of pharyngeal process of the basioccipital is joined laterally to the pharyngeal process of the parasphenoid. The bone is bounded anteriorly by the posterior prootic, laterally by the exoccipital (Fig. 6A).

Pungitius pungitius

The basioccipital is identical to *Culaea* (Fig. 6B).

Apeltes quadracus

The basioccipital is similar to the two previous

species (Fig. 6C).

Parasphenoid

Culaea inconstans

The parasphenoid is a remarkably long bone and covers the ventral surface of the neurocranium for about four-fifths of its entire length (the anterior parasphenoid lies over the vomer). The bone consists of a long narrow body and two dorso-lateral ascending processes. The posterior process of the parasphenoid is called the pharyngeal process which is split (Fig. 7A). The lateral process of the parasphenoid is connected anteriorly with the sphenotic. The pharyngeal process of the parasphenoid is articulated laterally with prootic (Fig. 6A).

Pungitius pungitius

The parasphenoid is identical to *Culaea* (Fig. 6B).

Apeltes quadracus

The parasphenoid is similar to the two species mentioned above (Fig. 6C).

V. Branchiocranium

A. Hyobranchial region (Fig. 8, Fig. 9, Fig. 15D, Fig. 16D, Fig. 17D)

Interhyal

Culaea inconstans

The interhyal is a small rod-shaped bone connected at one end to the posterior margin of the epihyal. The other

end points posteriorly and loosely touches the dorsal process of the preopercular (Fig. 8, Fig. 15D).

Pungitius pungitius

The interhyal is identical in appearance to *Culaea* (Fig. 9, Fig. 16D).

Apeltes quadracus

The interhyal is identical to the two species mentioned above (Fig. 10, Fig. 17D).

Epihyal

Culaea inconstans

The epihyal is somewhat triangular. Half of the bone is underneath the posterior process of the elongate ceratohyal (Fig. 15D).

Pungitius pungitius

The epihyal is more or less similar to the previous species (Fig. 16D).

Apeltes quadracus

The epihyal is similar to both species mentioned above (Fig. 17D).

Ceratohyal

Culaea inconstans

The ceratohyal is a fairly large bone, basically the anterior portion is narrow while the posterior portion gradually expands. The posterior portion is nearly three times wider than the anterior end. The bone possesses the long posterior process (Fig. 15D).

Pungitius pungitius

There is no morphological difference between these two species (Fig. 16D).

Apeltes quadracus

The ceratohyal is similar to the two species mentioned above (Fig. 17D).

Hypohyal

Culaea inconstans

The hypohyal consists of two parts. The dorsal bone (Dorsal hypohyal) is triangular and the ventral bone (Ventral hypohyal) is shaped like a smoking pipe with its handle projecting posteriorly and touching along the ventral surface of the ceratohyal. The dorsal hypohyal is articulated posteriorly with the anterior ceratohyal. The hypohyal is connected anteriorly with the posterior end of the basihyal (Fig. 15D).

Pungitius pungitius

The hypohyal is identical to the previous species (Fig. 16D).

Apeltes quadracus

The hypohyal is similar to both species mentioned above (Fig. 17D).

Basihyal

Culaea inconstans

The basihyal (glossohyal) is a long, single, rod-like bone extending posteriorly. The bone articulates

postero-ventrally with the anterior end of the posterior basihyal (Fig. 15B).

The posterior basihyal is a single bone triangular in shape. The posterior end of the bone consists of two processes which form the spine (Fig. 15C).

Pungitius pungitius

The basihyal and posterior basihyal are similar to *Culaea* (Fig. 16C).

Apeltes quadracus

The basihyal and posterior basihyal are similar to the two species mentioned above (Fig. 17C).

Urohyal

Culaea inconstans

The urohyal is a long, single bone with a pointed end projecting posteriorly. It possesses ventro-lateral ridges on both sides. The ventral surface of the bone expands broadly. The bone is situated anteriorly underneath the postero-ventral surface of the posterior basihyal (Fig. 15B, Fig. 15C).

Pungitius pungitius

The urohyal is identical to the previous species (Fig. 16B, Fig. 16C).

Apeltes quadracus

The urohyal develops a very narrow ventral surface area (Fig. 17B, Fig. 17C), otherwise it is similar to *Culaea* and *Pungitius*.

Branchiostegal ray

Culaea inconstans

Three branchiostegal rays are present, each ray is a long slender bone projecting posteriorly and curving upward. The two most anterior rays are connected laterally with the ceratohyal, while the last long ray is articulated with the epihyal (Fig. 15D).

Pungitius pungitius

The three branchiostegal rays are similar to *Culaea* (Fig. 16D).

Apeltes quadracus

The three branchiostegal rays are similar to the two species mentioned above, except that the first ray is connected laterally with the ceratohyal while the two posterior rays join to the epihyal (Fig. 17D).

Basibranchial

Culaea inconstans

The two basibranchials are rod-shaped bones. They do not touch the hypobranchials.

Three pairs of hypobranchials are present. They are somewhat pulley-like in form, having identical plates on both dorsal and ventral surfaces. They touch loosely in between the ceratobranchials and the epibranchials.

Five pairs of ceratobranchials are present. The first four pairs of anterior ceratobranchials are very elongate, rod-shaped bones. The fifth paired ceratobranchial is expanded anteriorly with distinctive numerous sharp teeth

appearing on the dorsal surface. The gill rakers are present along both lateral margins of the ceratobranchials. The number of the gill rakers ranges from 10-12. They are found on each margin of the bone except that the gill rakers are present only on one side of the fifth pair of the ceratobranchial (Fig. 15A).

Pungitius pungitius

The two basibranchials and three hypobranchials are similar to *Culaea*. The five pairs of ceratobranchials are similar to *Culaea* in general appearance, except that the fifth pair lacks gill rakers. The gill rakers are present on both margins of the ceratobranchials. The number of the gill rakers ranges from 10-14. The prominent long gill rakers appear on the first pair of the ceratobranchials (Fig. 16A, Fig. 16B).

Apeltes quadracus

The two basibranchials are similar to the two species mentioned above. The hypobranchials are considerably larger than the two mentioned species. The third pair of hypobranchials appear to be rod-shaped bones (Fig. 17A, Fig. 17B).

There are five pairs of ceratobranchials. The fifth pair lacks gill rakers. The gill rakers are relatively short and small. There are 8 gill rakers on the ceratobranchial borders (Fig. 17A, Fig. 17B).

Epibranchial and Pharyngobranchial

Culaea inconstans

There are four pairs of epibranchials, the fifth epibranchial is wanting. The epibranchials are slender rod-shaped bones which are connected anteriorly to the posterior ceratobranchial. The first pair of epibranchials are larger than the rest and the bones appear without any projections. The second, third, and fourth pairs of epibranchials have conspicuous projections dorso-medially (Fig. 15A).

The first pharyngobranchial is absent. The second pharyngobranchial is a small plate-like element bearing teeth ventrally (the number of the teeth ranges between 4-6; the same number is found in *Apeltes*).

The third and fourth pharyngobranchials are fused and indistinguishable from one another. The ventral surface is covered with numerous, well-developed teeth (Fig. 15A).

Pungitius pungitius

The epibranchials are more or less similar to the previous species. The first pharyngobranchial is wanting. The second pharyngobranchial is identical to *Culaea*, except that the bone bears 10-16 sharp teeth (Fig. 16A).

Apeltes quadracus

The epibranchials are similar to the two species mentioned above. The first pharyngobranchial is absent. The second pharyngobranchial bears sharp teeth. The number of the teeth ranges between 4-6, the same number found in *Culaea* (Fig. 17A).

B. Opercular series (Fig. 8, Fig. 9, Fig. 10, Fig. 14, A,B,C)

Operculum

Culaea inconstans

The operculum is a remarkably large, triangular bone with the articular process appearing as an ear-like projection at the antero-dorsal corner of the bone. The entire anterior corner of the operculum articulates with the posterior head process of the hyomandibular, whereas the posterior border is broadly extended. The posterior margin is ragged, rather than continuous and smooth, consisting of squared off rod-like projections (Fig. 8, Fig. 14A).

The suboperculum appears as a long, sickle-shaped bone, with a convex ventral edge. The blade of the sickle curves in a postero-dorsal direction ending at a sharp point. The broad handle of the sickle curves upward and gradually more anteriorly, ending with a relatively straight basal margin (margin almost vertical, with the ventral corner more anterior than the dorsal corner) (Fig. 14A).

The interoperculum is an elongate, triangular-shaped bone with the ventral surface curved inwards and the elongate limb pointed anteriorly. The posterior margin and the most posterior border of the bone is opposed to the antero-ventral curvature of the suboperculum. The interoperculum lies internal to the preoperculum (Fig. 8, Fig. 14A).

The preoperculum is almost sickle-shaped, with two limbs, one pointing dorsally and the other anteriorly. The two limbs thus tend to give the postero-ventral corner of

the preoperculum somewhat of a right-angled shape ($>90^\circ$) (Fig. 14A).

Pungitius pungitius

The operculum is similar to *Culaea*, except the posterior margin of the bone is smooth (Fig. 14B).

The suboperculum looks the same as in *Culaea* whereas the antero-ventral surface of the suboperculum is somewhat convex, and is opposed ventrally to the posterior end of the interoperculum (Fig. 14B).

The interoperculum is identical to *Culaea*, except that the postero-ventral portion of the bone has a relatively long extension (Fig. 14B).

The preoperculum is more or less identical to the previous species (Fig. 14B).

Apeltes quadracus

The operculum is an axe-shaped bone, with a relatively straight posterior margin. The margin of the bone is smooth along the entire blade-like border.

The subopercular is similar to *Pungitius*, except that the posterior border of the bone is jagged. The bone overlaps anteriorly with the preoperculum and dorso-medially with the ventral corner of the operculum (Fig. 14C).

The interoperculum is similar to both species mentioned above. The posterior portion of the interoperculum is relatively round and slender in appearance (Fig. 14C).

The preoperculum is similar to *Culaea* and *Pungitius* (Fig. 10, Fig. 14C).

VI. Oromandibular region (Fig. 3, A,B,C; Fig. 5, A,B,C;
 Fig. 6, A,B,C; Fig. 8, Fig. 9,
 Fig. 10, Fig. 13, A,B,C; Fig.
 14, A,B,C).

Palatine and Entopterygoid

Culaea inconstans

The palatine is a slender curved bone, connecting antero-laterally to the posterior end of mesethmoid, dorsally to the ventral surface of the lateral ethmoid, laterally to the pachrymal, posteriorly to the entopterygoid. The body of the palatine among the three species is similar (Fig. 13, A,B,C).

The ectopterygoid is absent among the three species.

The entopterygoid is a broad thin bone. It is bordered anteriorly by the palatine and ventrally by the triangular-shaped quadrate. The posterior end of the entopterygoid does not reach the anterior symplectic floor. There is a big gap between the posterior entopterygoid and the anterior symplectic (Fig. 13A).

Pungitius pungitius

The postero-ventral part of the entopterygoid overlaps the antero-dorsal floor of the symplectic (Fig. 13B, Fig. 14B).

Apeltes quadracus

The entopterygoid is similar to *Pungitius* (Fig. 13C, Fig. 14C).

Metapterygoid

Culaea inconstans

The metapterygoid is variable in shape. It articulates antero-ventrally with the postero-dorsal surface of the symplectic and posteriorly with the hyomandibular (Fig. 13A, Fig. 14A).

Pungitius pungitius

The metapterygoid is similar to *Culaea* (Fig. 13B, Fig. 14B).

Apeltes quadracus

The metapterygoid is identical to the two species mentioned above (Fig. 13C, Fig. 14C).

Symplectic

Culaea inconstans

The symplectic is a relatively large, elongate, curved bone. It is a single piece of bone but it seems to consist of three different bones. The bone is articulated anteriorly with quadrate and dorsally with the ventral surface of the metapterygoid. The anterior symplectic rests on the posterior process of the quadrate (Fig. 13A, Fig. 14A).

Pungitius pungitius

The symplectic is identical to *Culaea*, except that the anterior end of the symplectic reaches and joins with the postero-ventral surface of the entopterygoid (Fig. 13B, Fig. 14B).

Apeltes quadracus

The symplectic is similar to *Pungitius* (Fig. 13C, Fig.

14C) .

Quadrate

Culaea inconstans

The quadrate is more or less a quadrangular bone with its antero-ventral corner modified into a condyle. The dorsal border of the bone is convex. The bone is articulated dorsally with the entopterygoid. The posterior edge of the bone extends posteriorly to form a long prominent dorsal process of a drain-pipe-like bone and joins posteriorly to the quadrate and the anterior portion of the simplectic (Fig. 13A) .

Pungitius pungitius

The quadrate is identical to *Culaea* (Fig. 13B) .

Apeltes quadracus

. The quadrate is similar to both species mentioned above (Fig. 13C) .

Hyomandibular

Culaea inconstans

The hyomandibular consists of a body with an anterior articular head, dorsal articular head, and posterior articular head. The anterior head forms an extra broad process, projecting anteriorly, and articulated with the metapterygoid. The anterior head of the hyomandibular is articulated with the sphenotic, the dorsal head is articulated with the pterotic, and the posterior head of the bone is connected with an articular facet which is situated

on the medial surface in the antero-dorsal corner of the operculum. The posterior head of the hyomandibular forms a prominent posterior process projecting downwards which is situated underneath the preoperculum (Fig. 14A).

Pungitius pungitius

The hyomandibular is similar to *Culaea* (Fig. 14B).

Apeltes quadracus

The hyomandibular is identical to the two species mentioned above (Fig. 14C).

Premaxillary

Culaea inconstans

The premaxillary possesses prominent teeth and a well-developed ascending process.

The toothless maxillary is a slender bone. The anterior dorsal part of the bone loosely touches the ascending process of the premaxillary. It is a moveable bone which assists the premaxillary in projecting out for feeding purposes (Fig. 3A, Fig. 5A, Fig. 6A, Fig. 8).

Pungitius pungitius

The premaxillary and the maxillary are similar to *Culaea* (Fig. 3B, Fig. 5B, Fig. 6B, Fig. 9).

Apeltes quadracus

The premaxillary and the maxillary are similar to both species mentioned above (Fig. 3C, Fig. 5C, Fig. 6C, Fig. 10).

Angular

Culaea inconstans

The angular is dart-like in appearance. It has a prominent pointed process anteriorly. The postero-dorsal end of the dentary lies over the anterior process of the angular. The postero-ventral arm of the dentary does not touch the antero-ventral corner of the angular as it does in both *Pungitius* and *Apeltes*. The postero-dorsal process of the angular is rather pointed. The postero-dorsal process of the angular does not reach the postero-dorsal dentary. Postero-ventrally, the angular is reduced to a long slender process on which the antero-ventral condyle of the quadrate rests (Fig. 14A).

Pungitius pungitius

The angular is similar to *Culaea* (Fig. 14B).

Apeltes quadracus

The angular is similar to the two species, except that the postero-dorsal process of the bone is relatively blunt and overlaps the dorso-posterior process of the dentary (Fig. 14C).

Dentary

Culaea inconstans

The dentary is a strong, large bone possessing prominent teeth along the antero-dorsal portion of the bone. The posterior end consists of two different parts, the long and strong postero-dorsal process and the slender elongate postero-ventral process which does not touch the antero-

ventral corner of the angular (it does not touch the anterior margin of the retroarticular (Fig. 14A)).

Pungitius pungitius

The dentary is similar to *Culaea*, except that the posterior arm of the bone reaches the retroarticular (Fig. 14B).

Apeltes quadracus

The dentary is similar to *Culaea* and *Pungitius*, except that the ventral process of the bone touches the ventral corner of the angular and the retroarticular (Fig. 14C).

Retroarticular

Culaea inconstans

The retroarticular is a small triangular-shaped bone. It fits against the postero-ventral corner of the angular. It is also a cup-shaped bone with the open mouth on the dorsal surface. The ventral corner of the bone is projecting downward (Fig. 13A).

Pungitius pungitius

The retroarticular is identical to *Culaea* (Fig. 13B).

Apeltes quadracus

The retroarticular is more or less similar in general appearance to the two species mentioned above (Fig. 13C).

DISCUSSION AND CONCLUSIONS

A general summary of the morphological differences of the cranial skeleton of the three species of sticklebacks, *Culaea inconstans*, *Pungitius pungitius*, and *Apeltes quadracus* is presented below.

Culaea inconstans can be distinguished from *Pungitius pungitius* as follows:

Name of the Bone	<i>Culaea inconstans</i>	<i>Pungitius pungitius</i>
Nasal	is shorter and the ventral process is smaller (Fig. 3A, Fig. 5A).	is longer and the ventral process is larger (Fig. 3B, Fig. 5B).
mes-ethmoid	is shorter (Fig. 12A).	is longer and slimmer (Fig. 12B).
single ethmoid	is a small circular shaped bone (Fig. 12A).	is an oval-shaped bone with the wider part on the dorsal portion (Fig. 12B).
Frontal	is short (Fig. 3A, Fig. 5A).	is long (Fig. 3B, Fig. 5B).
Lachrymal	a deep indentation appears on the antero-dorsal surface (Fig. 8, Fig. 11A).	lacks indentation (Fig. 9, Fig. 11B).
Suborbitals	are usually three	are three in number

Name of the Bone	<i>Culaea inconstans</i>	<i>Pungitius pungitius</i>
	in number (including the lachrymal). The last one has several shallow lobes along the posterior margin (Fig. 11A).	(including the lachrymal). The last one is dichotomously branched on the posterior margin (Fig. 11B).
Supraoccipital	has a relatively short dorso-medial process (Fig. 3B, Fig. 4A).	has a long dorso-medial process (Fig. 3B, Fig. 4B).
Exoccipital	has a relatively short postero-dorsal wing (Fig. 3A, Fig. 4A).	has a long postero-dorsal wing (Fig. 3B).
Gill rakers	are short, the number ranges from 10-12 found on both margins of the ceratobranchial (Fig. 15A).	are long, the number ranges from 10-14 (Fig. 16A, Fig. 16B).
2nd Pharyngo-branchial	bears 4-6 ventral teeth (Fig. 15A).	bears 10-16 teeth on the ventral surface (Fig. 16A).
Operculum	has a ragged	has a round,

Name of the Bone	Superior View	Lateral View
	posterior margin (Fig. 8, Fig. 14A). margin with a continuously smooth border (Fig. 14B).	concave posterior margin with a continuously smooth border (Fig. 14B).
Suboperculum	is concave on the antero-ventral surface. The posterior margin is continuously smooth (Fig. 14A).	is convex on the antero-ventral surface and is continuously smooth on the posterior margin (Fig. 14B).
Interoperculum	possesses somewhat of a vertical margin posteriorly (Fig. 14A).	possesses a long extension on the postero-ventral portion (Fig. 14B).
Entopterygoid	does not reach to the symplectic floor (Fig. 13A, Fig. 14A).	overlaps the symplectic (Fig. 13B, Fig. 14B).

Culaea inconstans can be distinguished from *Apeltes quadracus* as follows:

Name of the Bone	<i>Culaea inconstans</i>	<i>Apeltes quadracus</i>
Mes-ethmoid	is longer (Fig. 12 A).	is shorter (Fig. 12 C).
Lateral ethmoid	has a small dorsal process and a small ventro-medial funnel shaped bone (Fig. 12A).	has a remarkably large dorsal flap-like process and a fairly broad part of the ventro-medial lip of funnel (Fig. 12C).
Single ethmoid	a small circular bone (Fig. 12A).	a large oval-shaped bone (Fig. 12C).
Vomer head	is more or less a square-shaped bone (Fig. 7A).	is somewhat long and rectangular (Fig. 7C).
Frontal	bears a spine-like process on the postero-lateral corner (Fig. 3B, Fig. 5B).	bears a blunt process on the postero-lateral corner (Fig. 3C, Fig. 5C).
Lachrymal	relatively smaller with a deep indentation on the antero dorsal surface (Fig. 8, Fig. 11A).	relatively larger without a deep indentation (Fig. 10, Fig. 11C).

Name of the Bone	<i>Culaea inconstans</i>	<i>Apeltes quadracus</i>
	area (Fig. 15B, Fig. 15C).	area (Fig. 17B, Fig. 17C).
Brancheostegal rays	The two anterior rays are connected laterally with the ceratohyal, while the last one is joined to the epihyal (Fig. 15D).	the first anterior ray is connected laterally with the ceratohyal while the two posterior rays are joined to the epihyal (Fig. 17D).
Gill rakers	the number ranges from 10-12. They are found on both margins of the ceratobranchial (Fig. 15A).	are very short, there are 8 gill rakers on each margin of the cerato- branchial (Fig. 17A).
Operculum	has a relatively concaved, ragged posterior margin (Fig. 8, Fig. 14A).	has a relatively straight, vertical margin which is continuously smooth (Fig. 14C).
Suboperculum	is concave on the antero-ventral surface. The post- erior margin is continuously smooth (Fig. 14A).	is relatively convex on the antero- ventral surface. The posterior margin is continuously ragged (Fig. 14C).

Name of the Bone	<i>Culaea inconstans</i>	<i>Apeltes quadracus</i>
Interoperculum	the posterior margin is almost vertical (Fig. 14A).	the posterior margin is convex (Fig. 14C).
Entopterygoid	does not reach to the symplectic floor (Fig. 13A, Fig. 14A).	overlaps the symplectic floor (Fig. 13C, Fig. 14C).
Angular	possesses a pointed postero-dorsal process (Fig. 14A).	bears a blunt postero-dorsal process (Fig. 14C).
Dentary	The dorsal process of the bone does not touch the postero-dorsal process of the angular (Fig. 14A).	The dorsal process of the bone is overlapped by the dorsal process of the angular (Fig. 14C).

Pungitius pungitius can be distinguished from *Apeltes quadracus* as follows:

Name of the Bone	<i>Pungitius pungitius</i>	<i>Apeltes quadracus</i>
Nasal	is longer (Fig. 3B) and the ventral process is larger (Fig. 5B).	is shorter (Fig. 3C) and the ventral process is smaller (Fig. 5C).
Mes-ethmoid	is longer and slimmer (Fig. 12B).	is relatively short (Fig. 12C).
Lateral ethmoid	is small and slender (Fig. 5B, Fig. 12B).	is larger with a remarkably large dorsal process and ventral tip of a funnel (Fig. 5C, Fig. 12C).
Single ethmoid	an oval-shaped bone with the wider part at the dorsal portion (Fig. 12B).	a large oval-shaped bone (Fig. 12C).
Vomer head	is a somewhat square-shaped bone (Fig. 7B).	is a somewhat long, rectangular bone (Fig. 7C).
Frontal	is long with a spine-like process on the postero-lateral corner (Fig. 3B, Fig. 5B).	is short, bearing a blunt process on the postero-lateral corner (Fig. 3C, Fig. 5C).

Name of the Bone	<i>Pungitius pungitius</i>	<i>Apeltes quadracus</i>
Lachrymal	is relatively small in size (Fig. 8, Fig. 11A).	is a remarkably large bone (Fig. 10, (Fig. 11C).
Suborbitals	are three in number (including the lachrymal). The last bone appears the dichotomous branchings on the posterior margin (Fig. 11B).	are usually two (including the lachrymal). The last has a relatively pointed end (Fig. 11C).
Sphenotic	has a pointed anterior process (Fig. 5B, Fig. 9).	has a blunt anterior process (Fig. 5C, Fig. 10).
Supraoccipital	has a relatively short dorsal-medial process (Fig. 3A, Fig. 4A).	has a very strong dorsal spine-like process (Fig. 10).
Exoccipital	has a long postero-dorsal wing (Fig. 3B).	has a very short postero-dorsal wing (Fig. 3C).
Sphenotic	} are separated (Fig. 6B).	} are suturally joined (Fig. 6C).
Prootic		
Pterotic		
Exoccipital		
Basioccipital		

Name of the Bone	<i>Ramphitrogonus</i>	<i>Apeltes quadracus</i>
Urohyal	has a broad ventral surface area (Fig. 16B, Fig. 16C).	has a very narrow ventral surface area (Fig. 17B, Fig. 17C).
Brancheostegal rays	The two anterior rays are connected laterally with the ceratohyal, while the last one is connected with the epihyal (Fig. 16D).	The first anterior is connected laterally with the ceratohyal while the two posterior rays are joined to the epihyal (Fig. 17D).
Gill rakers	are extremely long, the number ranges from 10-14 (Fig. 16A, Fig. 16B).	are very short. There are 8 gill rakers on each side of the ceratobranchial (Fig. 17A).
2nd Pharyngo-branchial	bears 10-16 teeth on the ventral surface (Fig. 16A).	bears 4-6 teeth on the ventral surface (Fig. 17A).
Operculum	has a relatively round edge or concave posterior margin with continuously smooth border (Fig. 14B).	has a relatively straight and vertical margin and continuously smooth (Fig. 14C).
Suboperculum	is convex on the antero-ventral	is ragged continuously on the

Name of the Bone	<i>Apeltes quadratus</i>	<i>Apeltes quadratus</i>
	surface. The posterior margin is continuously smooth (Fig. 14B).	posterior margin (Fig. 14C).
Interoperculum	possesses a long postero-ventral extension (Fig. 14B).	possesses a convex posterior border (Fig. 14C).
Angular	bears a pointed postero-dorsal process (Fig. 14B).	possesses a blunt postero-dorsal process (Fig. 14C).
Dentary	The dorsal process of the bone does not touch the postero-dorsal process of the angular (Fig. 14B).	The dorsal process of the bone is overlapped by the dorsal process of the angular (Fig. 14C).

There is no cranial bone that is unique to any of the three species. The only differences in the bones are differences of shape. In some cases, differences in number exist.

The morphological differences between the three species, *Culaea inconstans*, *Pungitius pungitius*, and *Apeltes quadracus* have been characterized by the distinctive features given below.

It is suggested that *Apeltes quadracus* possesses the most distinctive characteristics and is more specialized than *Culaea* and *Pungitius*. *Apeltes* has a reduction in the number of the following: gill rakers on the ceratobranchials, the suborbitals, and the teeth on the second pharyngobranchial. *Apeltes* also has the following bones reduced in size: mes-ethmoid, nasal, frontal and gill rakers (Fig. 3C, Fig. 5C, Fig. 10, Fig. 11C, Fig. 17A).

Culaea is characterized by the following distinctive features:

1. The single ethmoid is a small circular bone with lateral wing-like processes (Fig. 12A).
2. The lachrymal bears a deep indentation on the antero-dorsal surface (Fig. 8, Fig. 11A).
3. The suborbitals are usually three in number (including the lachrymal). The last bone possesses several shallow lobes along the posterior margin (Fig. 11A).
4. Gill rakers are relatively short; the number ranges from 10-12 and are found on both margins of the ceratobranchial

(Fig. 15A).

5. The second pharyngobranchial has 4-6 prominent teeth on the ventral surface (Fig. 15A).
6. The operculum has a ragged posterior border (Fig. 8, Fig. 14A).
7. Entopterygoid does not reach the symplectic floor (Fig. 13A, Fig. 14A).

Pungitius can be characterized by the following distinctive features:

1. The nasal is long and slender with a large process (Fig. 3B, Fig. 5B).
2. The single ethmoid is an oval-shaped bone with the widest part on the dorsal portion (Fig. 12B).
3. The frontal is remarkably long (Fig. 3B, Fig. 5B).
4. The suborbitals are usually three in number (including the lachrymal). The last one is dichotomously branched on the posterior margin (Fig. 11B).
5. Gill rakers are very long. The number ranges from 10-14 (Fig. 16A, Fig. 16B).
6. The second pharyngobranchial bears 10-16 prominent teeth on the ventral surface (Fig. 16A).

Apeltes is characterized by the following distinctive features:

1. The mes-ethmoid is short (Fig. 12C).
2. The lateral ethmoid has a long dorsal, flap-like process, and a large broad ventro-medial tip on the funnel (Fig. 12C).

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FIGURE 1. Location of Astotin Lake, Elk Island National Park, in relation to the City of Edmonton, Alberta (after Lin, 1968).

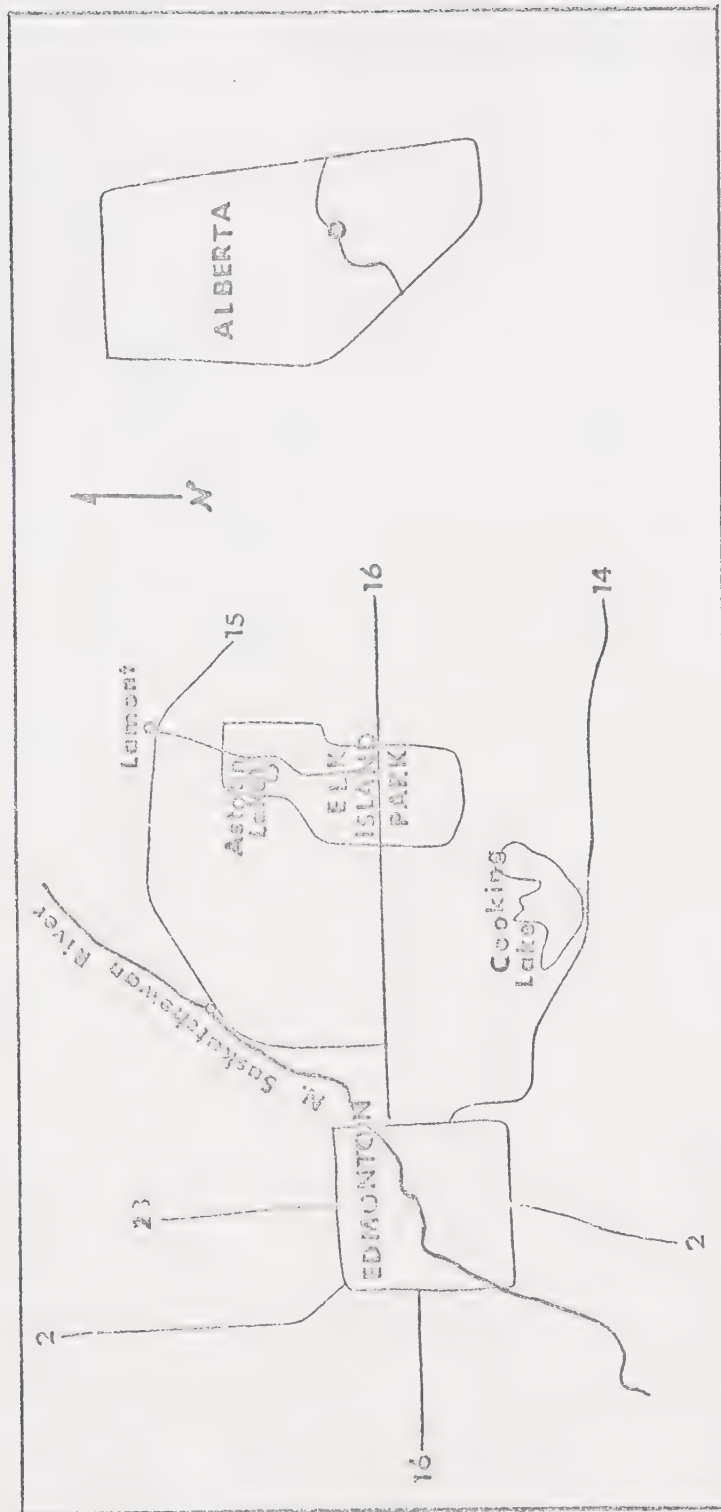


FIGURE 2. Residence Point, Astotin Lake, Elk Island
National Park, Alberta (after Smiley, 1972).



FIGURE 3.

A. Dorsal aspect of neurocranium of *Culaea inconstans*

(Sl. 36 mm)

B. Dorsal aspect of neurocranium of *Pungitius pungitius*

(Sl. 34 mm)

C. Dorsal aspect of neurocranium of *Apeltes quadracus*

(Sl. 35 mm)

Terminology:

1. nasal
2. mes-ethmoid
3. lateral ethmoid
4. single ethmoid
5. vomer head
6. frontal
9. sphenotic
10. pterotic
11. parietal
13. epiotic
17. supraoccipital
18. exoccipital
44. premaxillary
45. maxillary

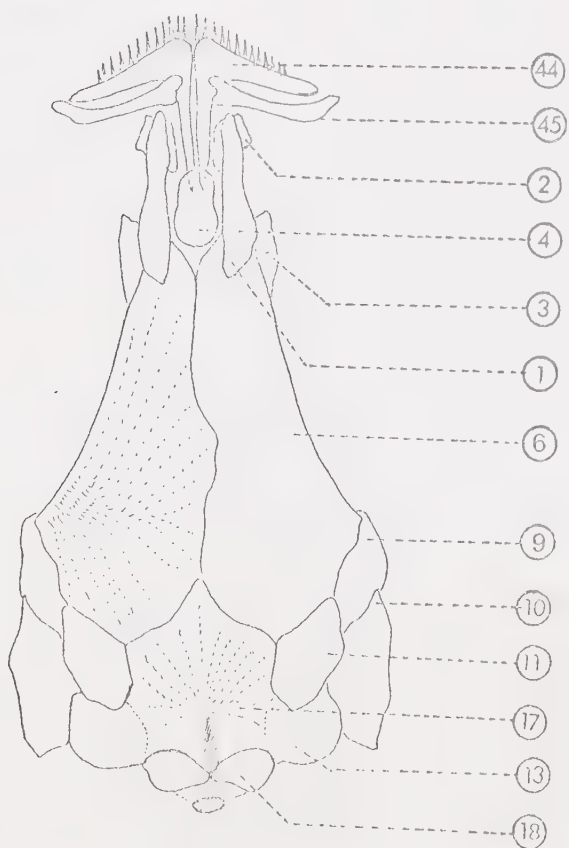
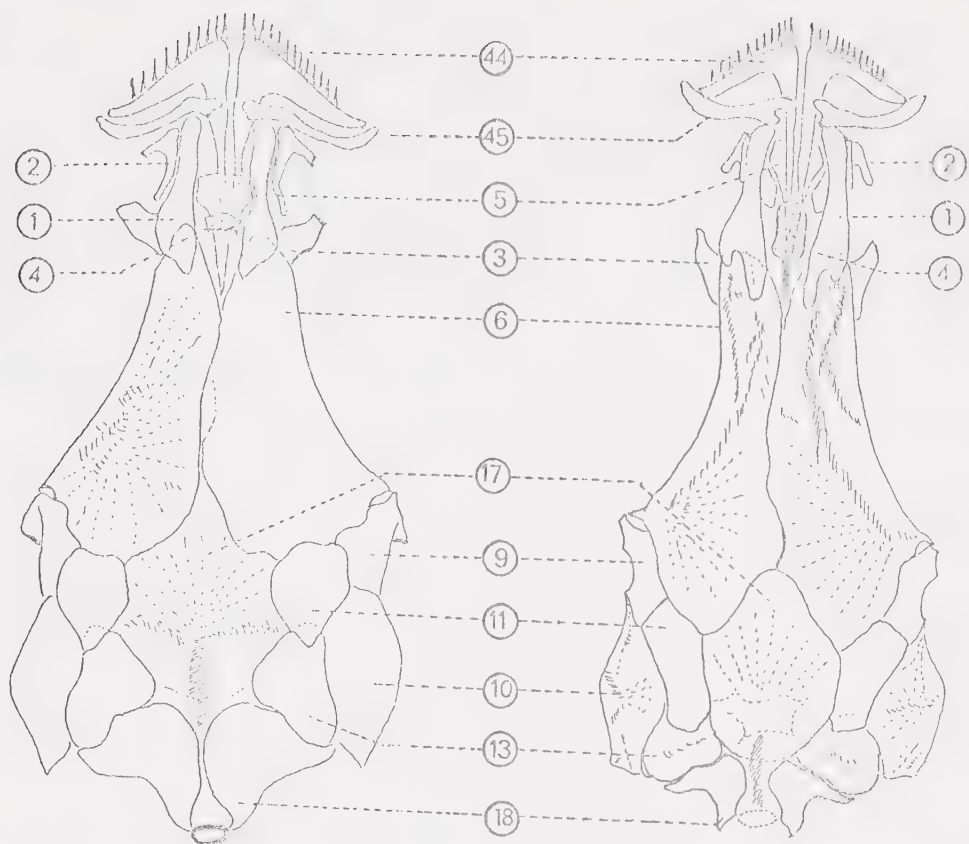


FIGURE 4.

A. Posterior aspect of neurocranium of *Culaea inconstans*

(Sl. 33 mm)

B. Posterior aspect of neurocranium of *Pungitius pungitius*

(Sl. 32 mm)

C. Posterior aspect of neurocranium of *Apeltes quadracus*

(Sl. 34 mm)

Terminology:

10. pterotic

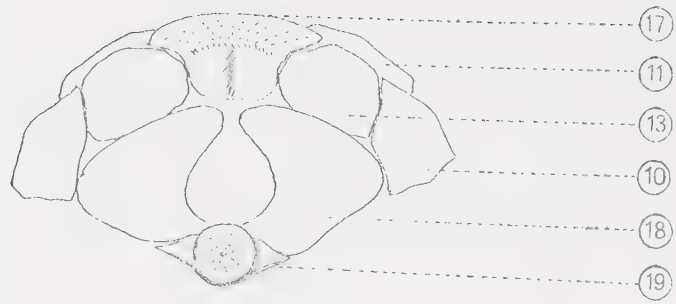
11. parietal

13. epiotic

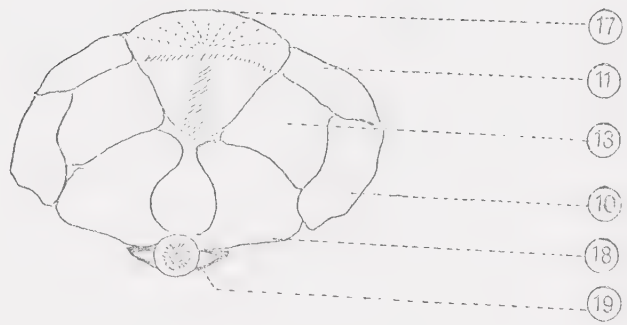
17. supraoccipital

18. exoccipital

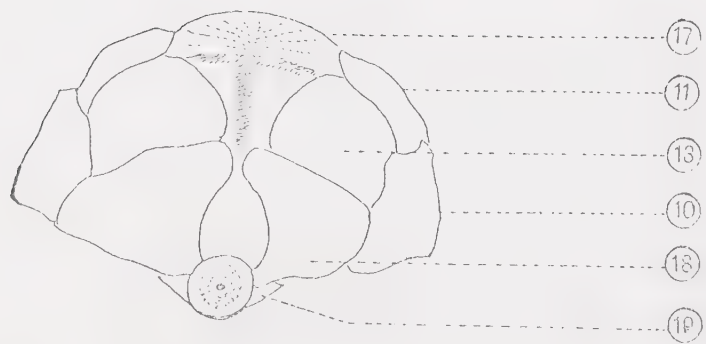
19. basioccipital



A



B



C

FIGURE 5.

A. Lateral aspect of neurocranium of *Culaea inconstans*

(Sl. 36 mm)

B. Lateral aspect of neurocranium of *Pungitius pungitius*

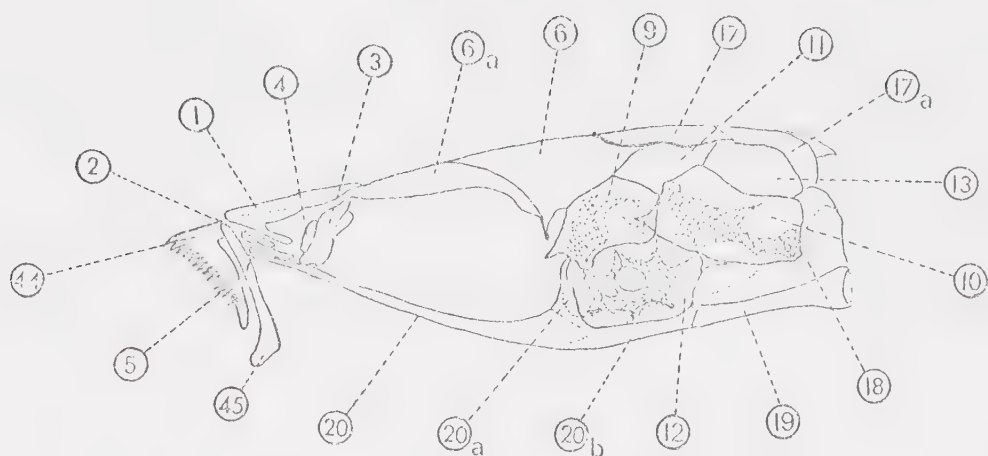
(Sl. 34 mm)

C. Lateral aspect of neurocranium of *Apeltes quadracus*

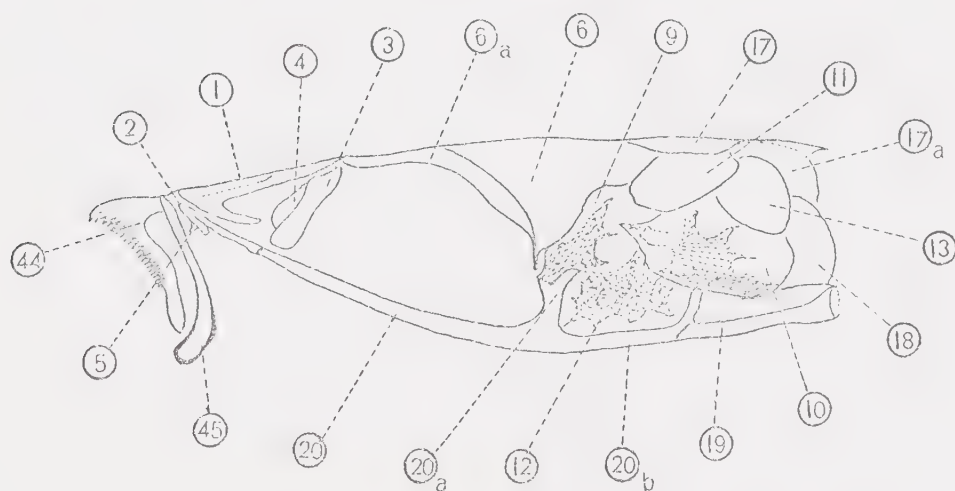
(Sl. 35 mm)

Terminology:

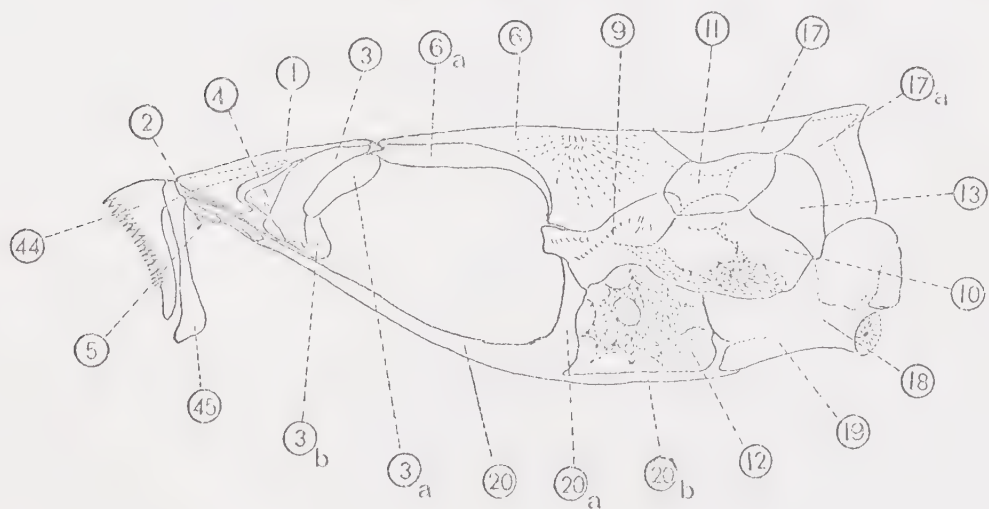
- | | |
|---|----------------------------|
| 1. nasal | 18. exoccipital |
| 2. mes-ethmoid | 19. basioccipital |
| 3. lateral ethmoid | 20. parasphenoid |
| 3a. lateral ethmoid process (flap-like) | 20a. lateral process of |
| 3b. lateral ethmoid process (bell-shaped) | parasphenoid |
| 4. single ethmoid | 20b. pharyngeal process of |
| 5. vomer | parasphenoid |
| 6. frontal | 44. premaxillary |
| 6a. frontal process | 45. maxillary |
| 9. sphenotic | |
| 10. pterotic | |
| 11. parietal | |
| 12. prootic | |
| 13. epiotic | |
| 17. supraoccipital | |
| 17a. supraoccipital process | |



A.



B.



C.

FIGURE 6.

A. Ventral aspect of neurocranium of *Culaea inconstans*

(Sl. 36 mm)

B. Ventral aspect of neurocranium of *Pungitius pungitius*

(Sl. 34 mm)

C. Ventral aspect of neurocranium of *Apeltes quadracus*

(Sl. 35 mm)

Terminology:

1. nasal
2. mes-ethmoid
3. lateral ethmoid
4. single ethmoid
5. vomer head
6. frontal
- 6a. frontal process
9. sphenotic
10. pterotic
12. prootic
16. intercalary
18. exoccipital
19. basioccipital
20. parasphenoid
- 20a. lateral process of parasphenoid
- 20b. pharyngeal process of parasphenoid
44. premaxillary
45. maxillary

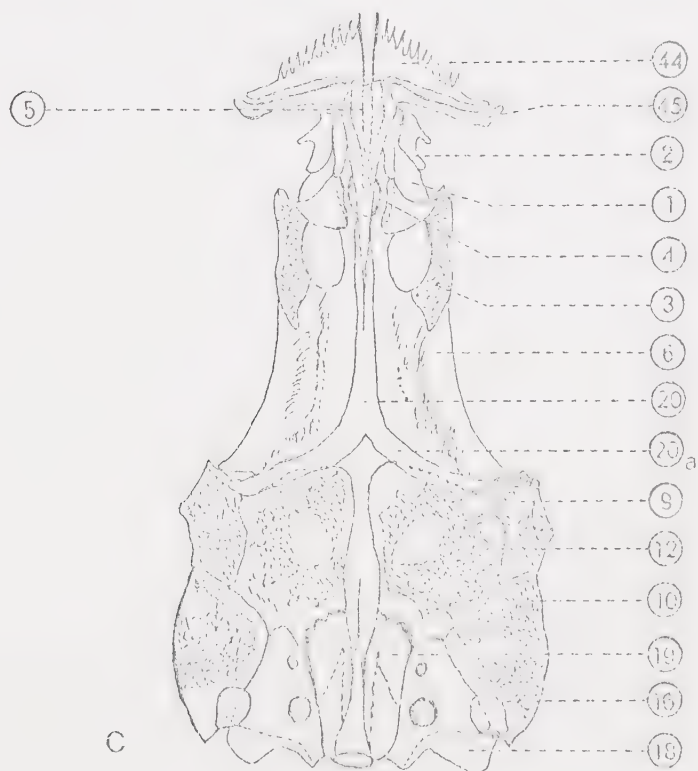
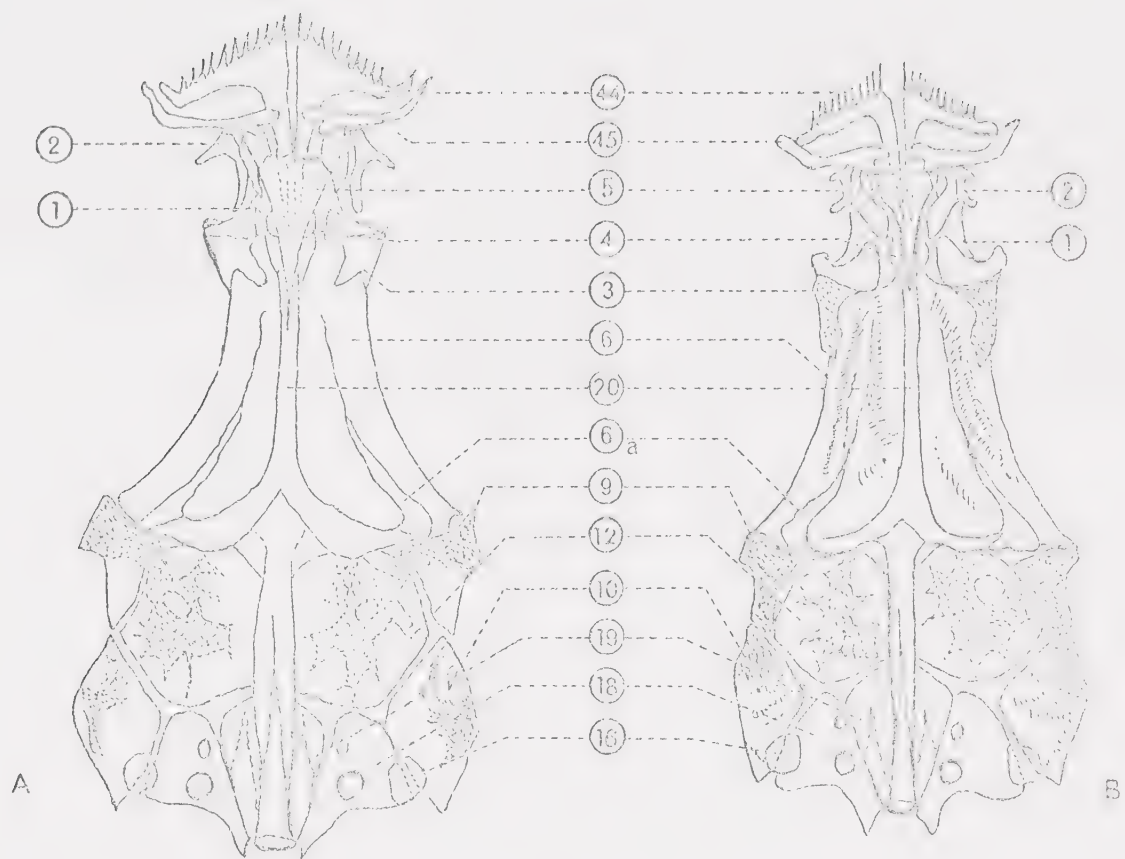


FIGURE 7.

A. Ventral aspect of parasphenoid of *Culaea inconstans*

(Sl. 38 mm)

B. Ventral aspect of parasphenoid of *Pungitius pungitius*

(Sl. 38 mm)

C. Ventral aspect of parasphenoid of *Apeltes quadracus*

(Sl. 38 mm)

Terminology:

- 5. vomer
- 19. basioccipital
- 20. parasphenoid
- 20a. lateral process of parasphenoid
- 20b. pharyngeal process of parasphenoid

FIGURE 8.

Lateral aspect of neurocranium of *Culaea inconstans*

(Sl. 35 mm)

Terminology:

- | | |
|-----------------------------|-------------------------|
| 1. nasal | 28. branchiostegal rays |
| 2. mes-ethmoid | 34. opercular |
| 3. lateral ethmoid | 35. subopercular |
| 4. single ethmoid | 36. interopercular |
| 5. frontal | 37. preopercular |
| 7. lachrymal | 40. metapterygoid |
| 8. suborbital | 41. symplectic |
| 9. sphenotic | 42. quadrate |
| 10. pterotic | 43. hyomandibular |
| 11. parietal | 44. premaxillary |
| 13. epiotic | 45. maxillary |
| 17. supraoccipital | 46. angular |
| 17a. supraoccipital process | 47. dentary |
| 18. exoccipital | 48. retroarticular |
| 19. basioccipital | |
| 20. parasphenoid | |
| 21. interhyal | |

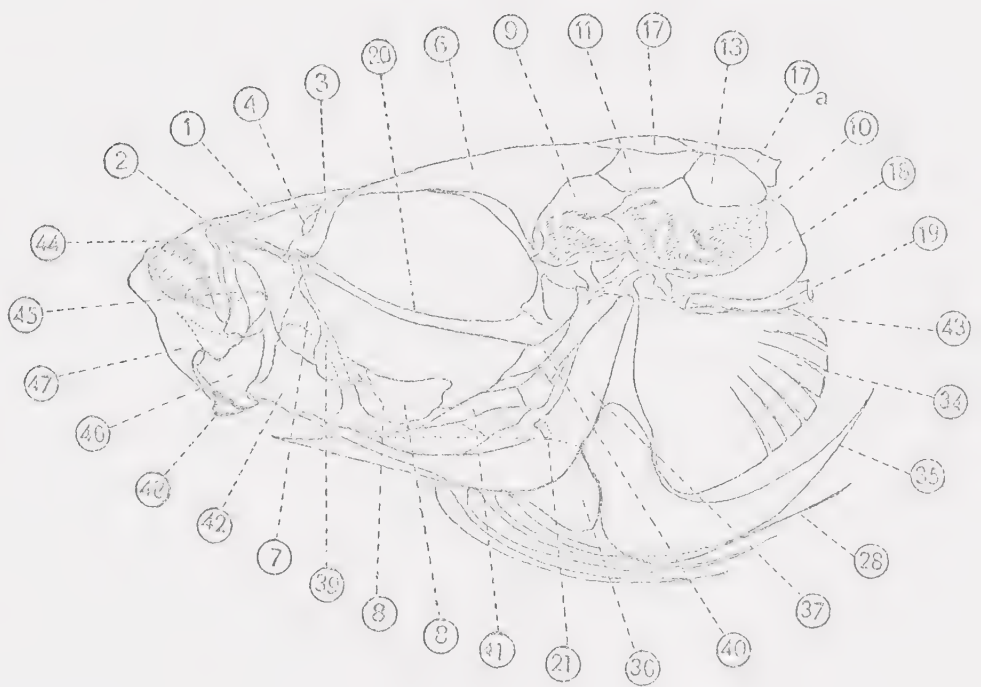


FIGURE 9.

Lateral aspect of neurocranium of *Pungitius pungitius*

(Sl. 35 mm)

Terminology:

- | | |
|-----------------------------|---------------------------|
| 1. nasal | 24b. ventral hypohyal |
| 2. mes-ethmoid | 25. basihyal (glossohyal) |
| 3. lateral ethmoid | 27. urohyal |
| 4. single ethmoid | 28. branchiostegal rays |
| 6. frontal | 34. opercular |
| 7. lachrymal | 35. subopercular |
| 8. suborbital | 36. interopercular |
| 9. sphenotic | 37. preopercular |
| 10. pterotic | 40. metapterygoid |
| 11. parietal | 41. symplectic |
| 13. epiotic | 42. quadrate |
| 14. posttemporal | 43. hyomandibular |
| 15. supracleithum | 44. premaxillary |
| 17. supraoccipital | 45. maxillary |
| 17a. supraoccipital process | 46. angular |
| 18. exoccipital | 47. dentary |
| 19. basioccipital | 48. retroarticular |
| 20. parasphenoid | |
| 21. interhyal | |
| 23. ceratohyal | |
| 24a. dorsal hypohyal | |

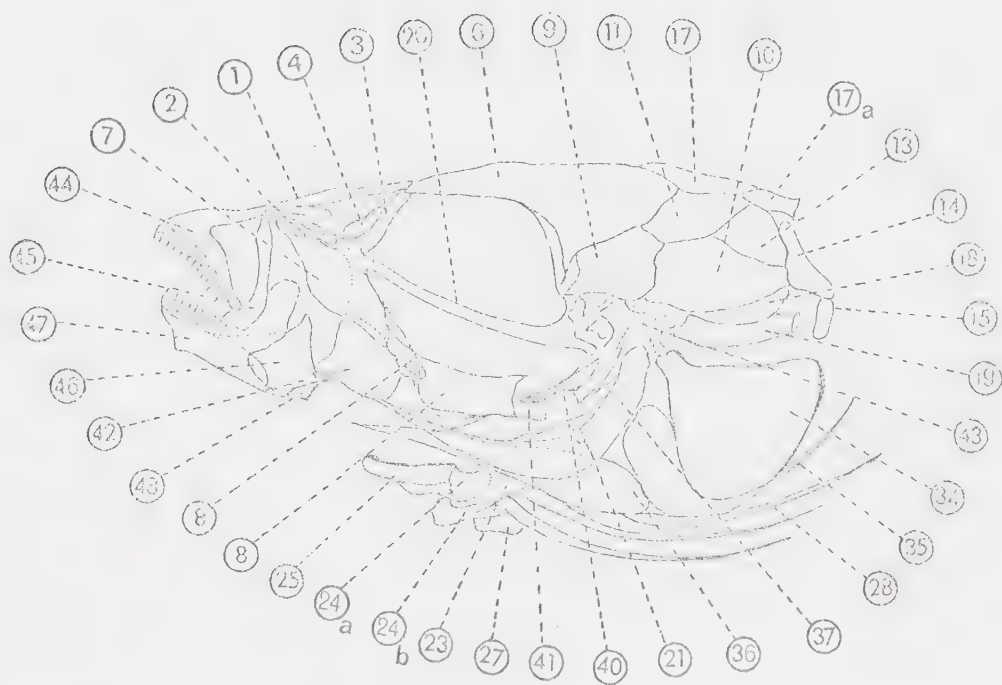


FIGURE 10.

Lateral aspect of neurocranium of *Apeltes quadracus*

(Sl. 35 mm)

Terminology:

- | | |
|-----------------------------|-------------------------|
| 1. nasal | 23. ceratohyal |
| 2. mes-ethmoid | 28. branchiostegal rays |
| 3. lateral ethmoid | 34. opercular |
| 4. single ethmoid | 35. subopercular |
| 6. frontal | 36. interopercular |
| 7. lachrymal | 37. preopercular |
| 8. suborbital | 40. metapterygoid |
| 9. sphenotic | 41. symplectic |
| 10. pterotic | 42. quadrate |
| 11. parietal | 43. hyomandibular |
| 13. epiotic | 44. premaxillary |
| 17. supraoccipital | 45. maxillary |
| 17a. supraoccipital process | 46. angular |
| 18. exoccipital | 47. dentary |
| 19. basioccipital | 48. retroarticular |
| 20. parasphenoid | |
| 21. interhyal | |

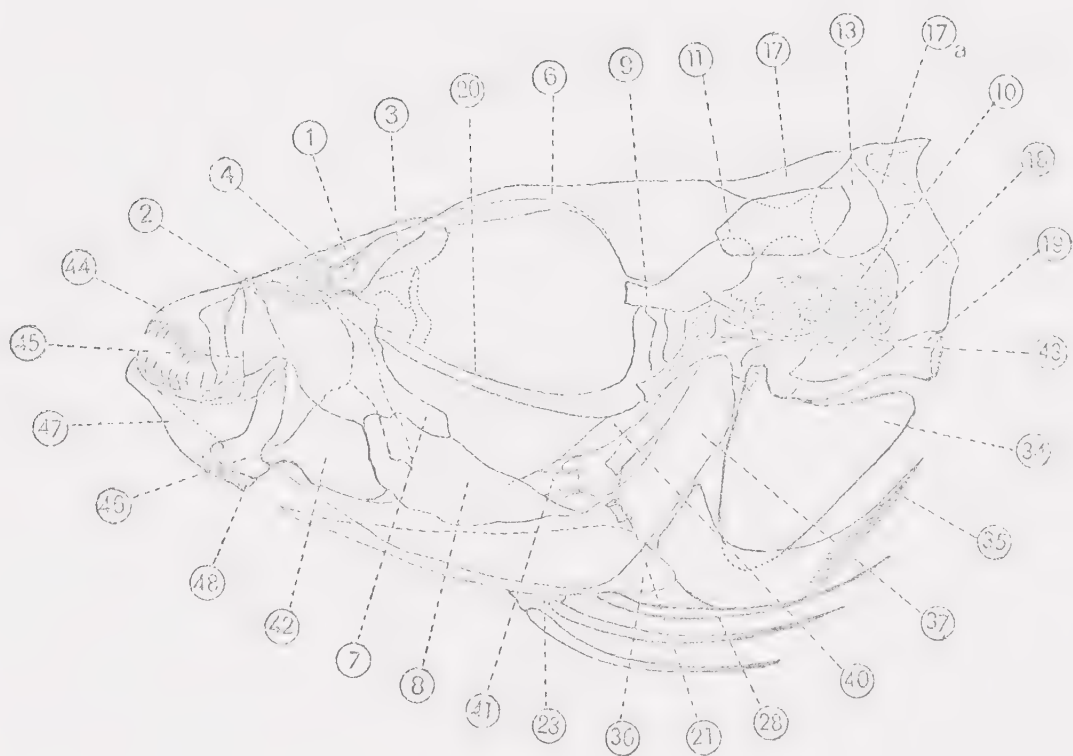


FIGURE 11.

A. Orbital region of *Culaea inconstans* (Sl. 38 mm)

B. Orbital region of *Pungitius pungitius* (Sl. 36 mm)

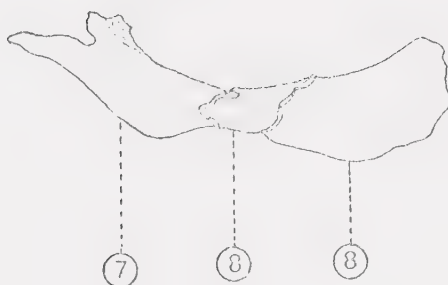
C. Orbital region of *Apeltes quadracus* (Sl. 37 mm)

Terminology:

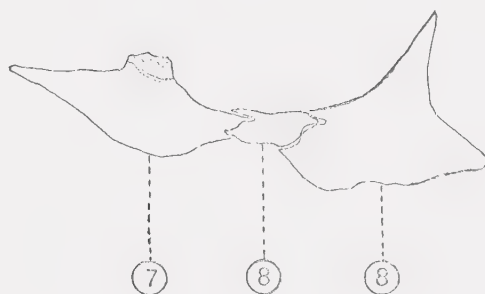
7. lachrymal

8. suborbital

A



B



C

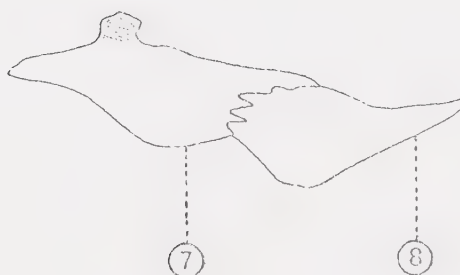


FIGURE 12.

A. Ventral aspect of ethmoid region of *Culaea inconstans*

(Sl. 36 mm)

B. Ventral aspect of ethmoid region of *Pungitius pungitius*

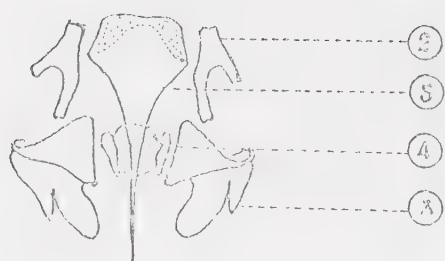
(Sl. 35 mm)

C. Ventral aspect of ethmoid region of *Apeltes quadracus*

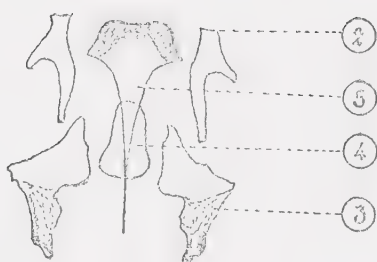
(Sl. 37 mm)

Terminology:

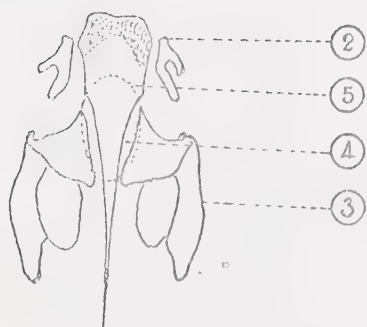
2. mes-ethmoid
3. lateral ethmoid
4. single ethmoid
5. vomer head



A



B



C

65.

FIGURE 14.

A. Lateral aspect of oromandibular region of *Culaea*

inconstans (Sl. 36 mm)

B. Lateral aspect of oromandibular region of *Pungitius*

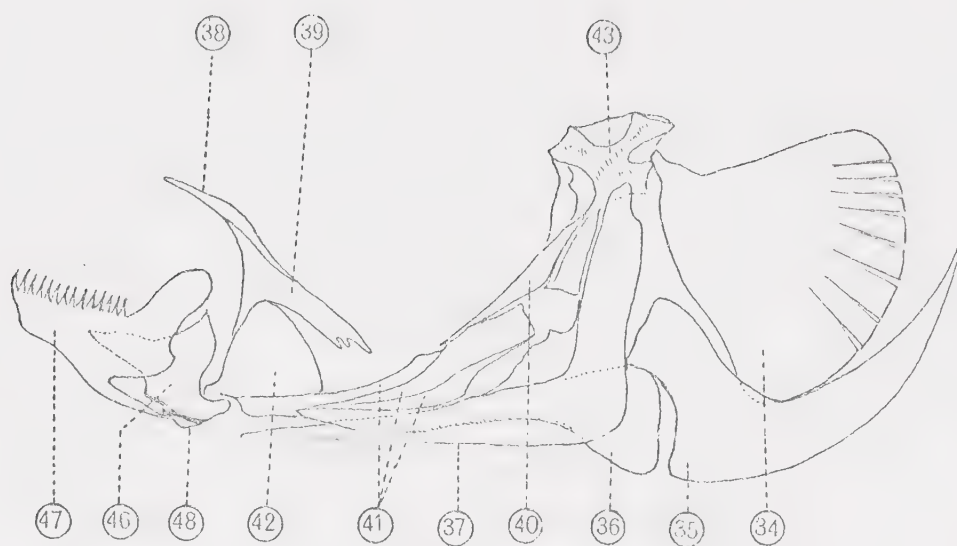
pungitius (Sl. 37 mm)

C. Lateral aspect of oromandibular region of *Apeltes*

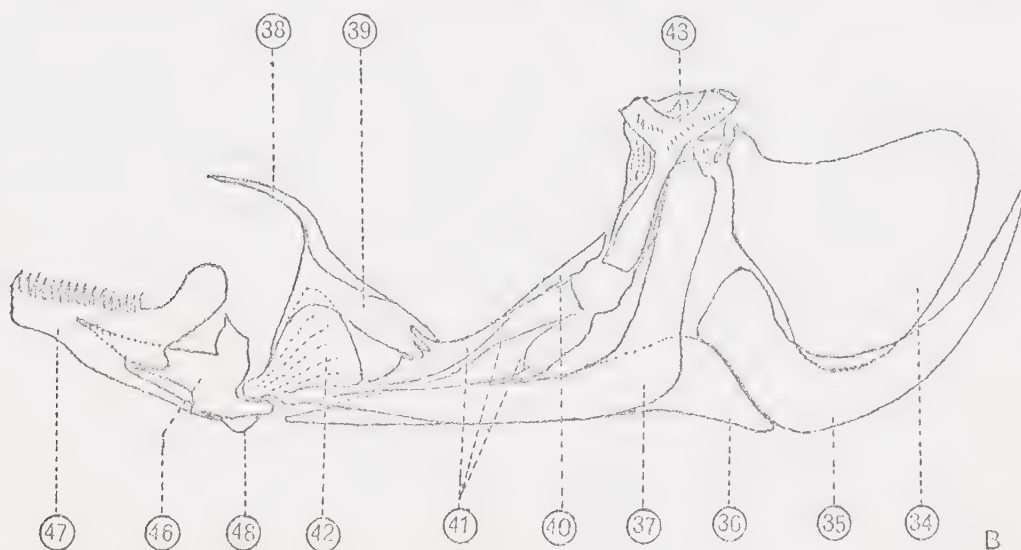
quadracus (Sl. 34 mm)

Terminology:

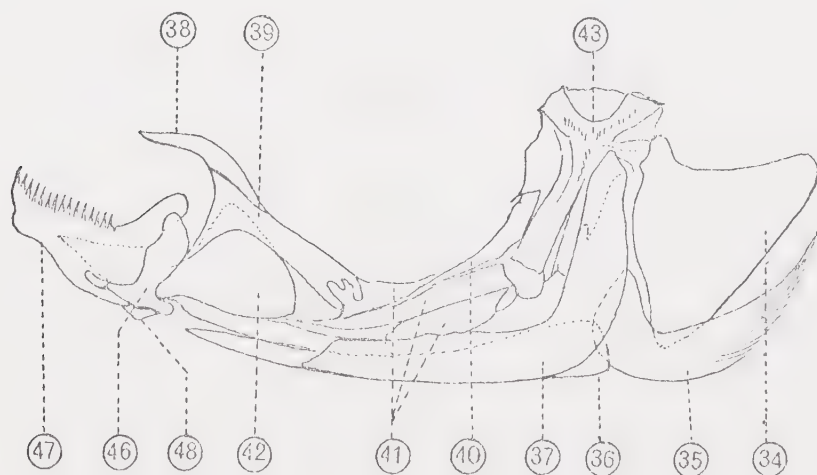
- 34. opercular
- 35. subopercular
- 36. interopercular
- 37. preopercular
- 38. palatine
- 39. entopterygoid
- 40. metapterygoid
- 41. symplectic
- 42. quadrate
- 43. hyomandibular
- 46. angular
- 47. dentary



A



B



C

FIGURE 15.

Hyobranchial region of *Culaea inconstans* (Sl. 41 mm)

- A. Dorsal aspect of hyobranchial region
- B. Ventral aspect of hyobranchial region
- C. Lateral aspect of basihyal and urohyal
- D. Lateral aspect of hyoid apparatus

Terminology:

- 21. interhyal
- 22. epihyal
- 23. ceratohyal
- 24a. dorsal hypohyal
- 24b. ventral hypohyal
- 25. basihyal (glossohyal)
- 26. posterior basihyal
- 27. urohyal
- 28. branchiostegal rays
- 29. basibranchial
- 30. hypobranchial
- 31. ceratobranchial
- 31a. gill raker
- 32. epibranchial
- 33. pharyngobranchial

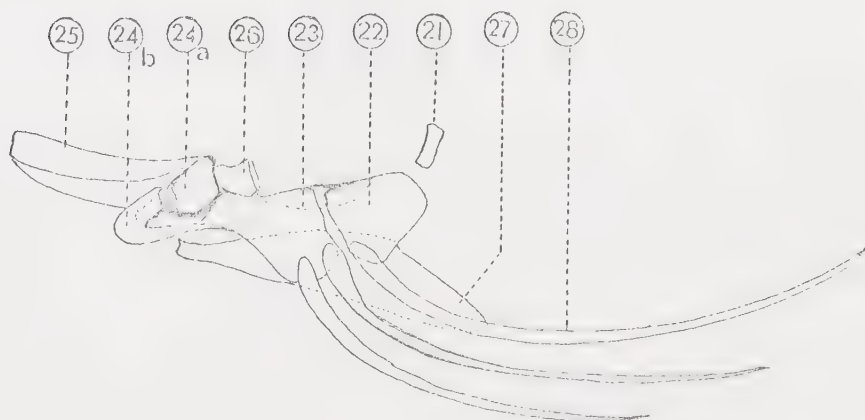
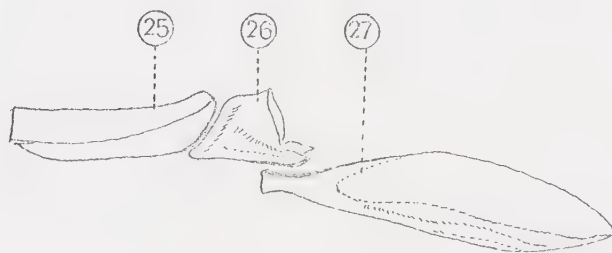
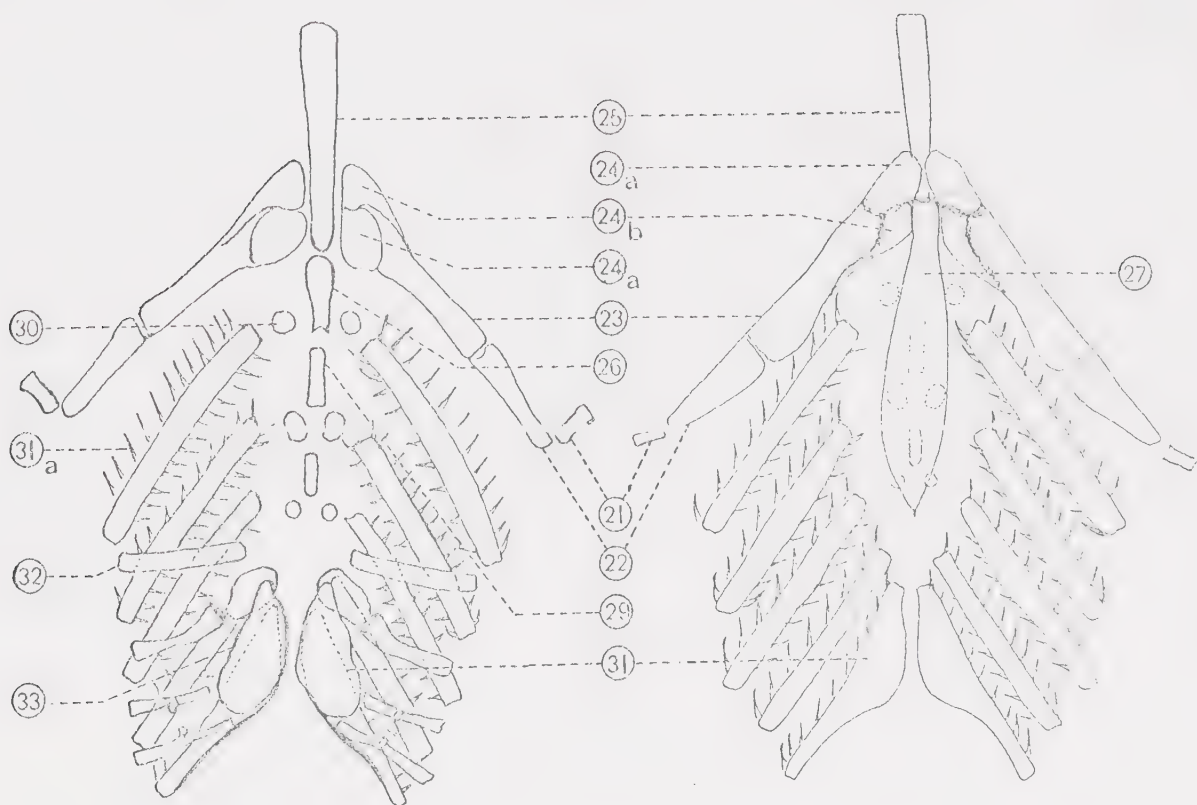


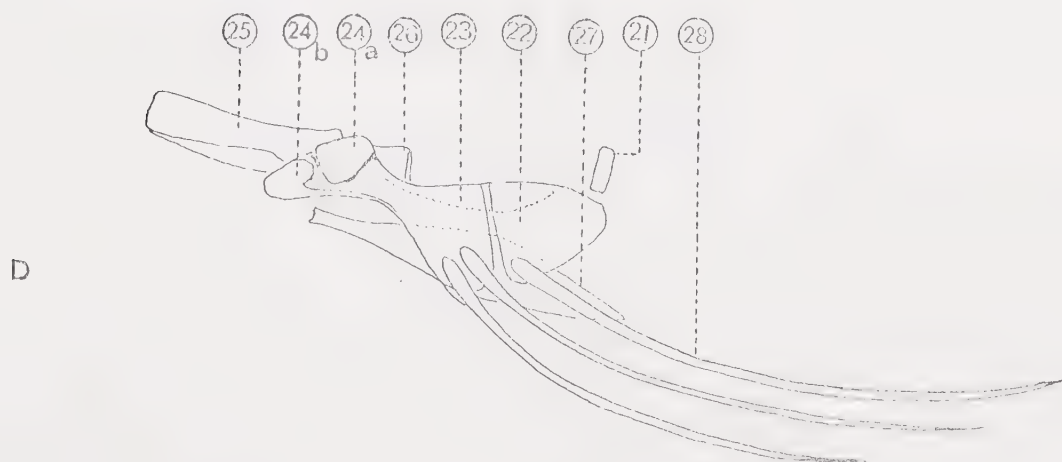
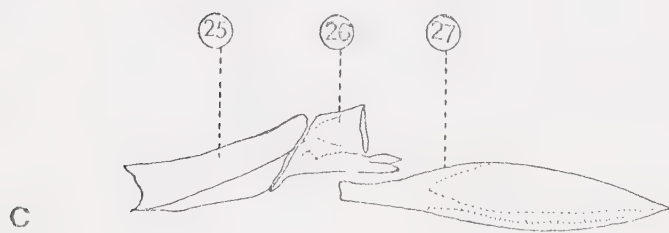
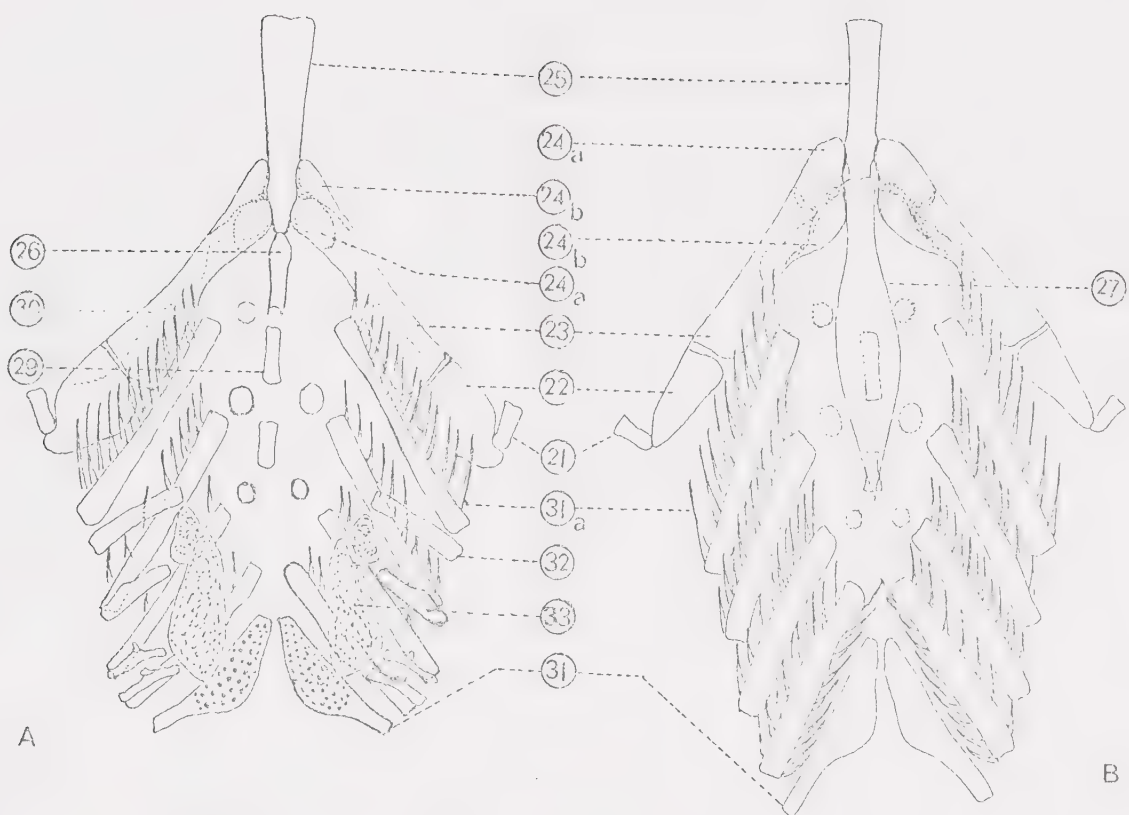
FIGURE 16.

Hyobranchial region of *Pungitius pungitius* (Sl. 40 mm)

- A. Dorsal aspect of hyobranchial region
- B. Ventral aspect of hyobranchial region
- C. Lateral aspect of basihyal and urohyal
- D. Lateral aspect of hyoid apparatus

Terminology:

- 21. interhyal
- 22. epihyal
- 23. ceratohyal
- 24a. dorsal hypohyal
- 24b. ventral hypohyal
- 25. basihyal (glossohyal)
- 26. posterior basihyal
- 27. urohyal
- 28. branchiostegal rays
- 29. basibranchial
- 30. hypobranchial
- 31. ceratobranchial
- 31a. gill raker
- 32. epibranchial
- 33. pharyngobranchial



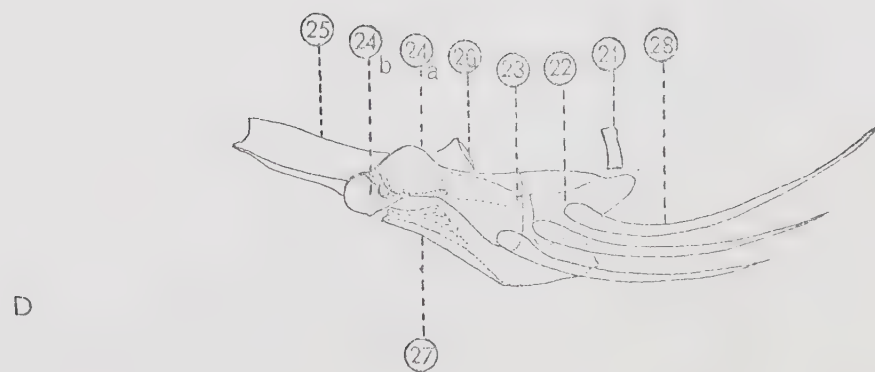
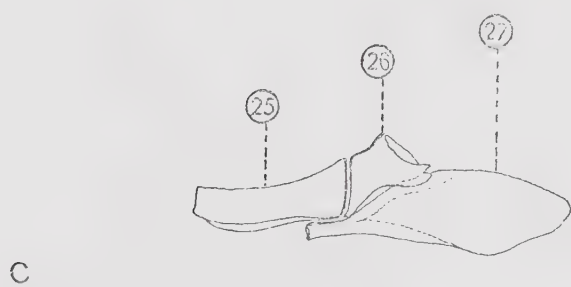
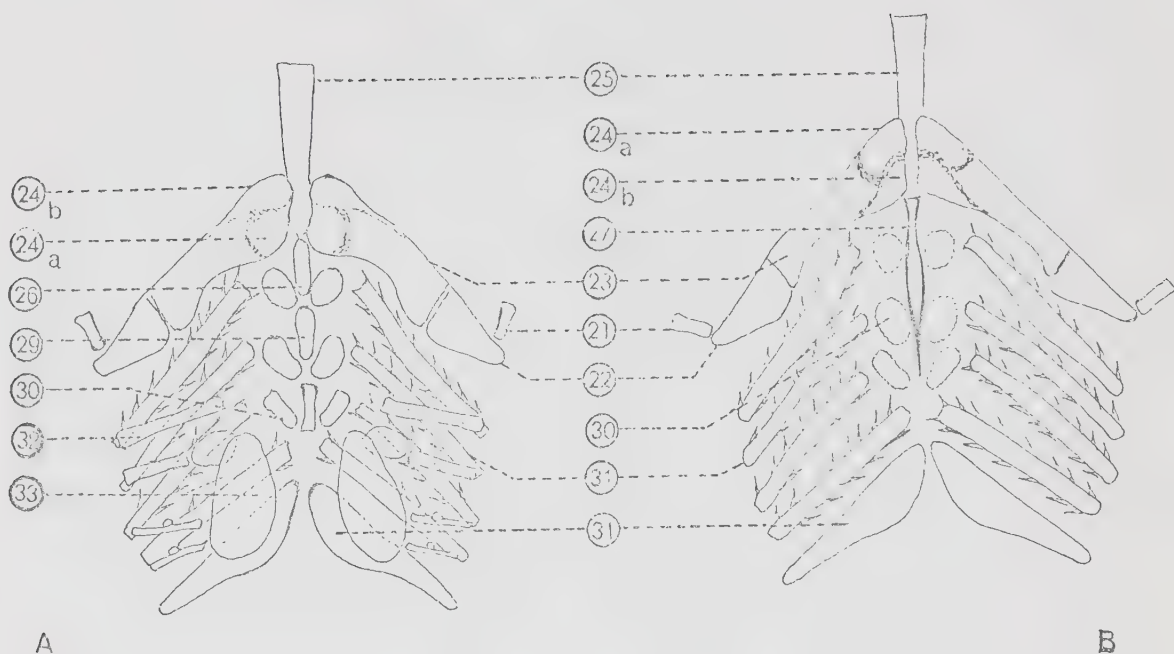


FIGURE 17.

Hyobranchial region of *Apeltes quadracus* (Sl. 36 mm)

- A. Dorsal aspect of hyobranchial region
- B. Ventral aspect of hyobranchial region
- C. Lateral aspect of basihyal and urohyal
- D. Lateral aspect of hyoid apparatus

Terminology:

- 21. interhyal
- 22. epihyal
- 23. ceratohyal
- 24a. dorsal hypohyal
- 24b. ventral hypohyal
- 25. basihyal (glossohyal)
- 26. posterior basihyal
- 27. urohyal
- 28. branchiostegal rays
- 29. basibranchial
- 30. hypobranchial
- 31. ceratobranchial
- 31a. gill raker
- 32. epibranchial
- 33. pharyngobranchial

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